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1 Haynes, C. V. *Science*, 166, 709–715 (1969).
2 Leakey, L. S. B., Simpson, R. DeE., and Clements, T., *Science*, 160, 1022–1033 (1968).
3 Haynes, C. V., *Science*, 181, 305–310 (1973).
4 Berger, R., and Libby, W. F., *Radiocarbon*, 11, 194–209 (1969).
5 Berger, R., Protsch, R., Reynolds, R., Rozair, C., and Sackett, J. R., *Contr. Univ. Calif. Archaeol. Res. Fac.*, No. 12, VI, 43–49 (1971).
6 Protsch, R., *J. Hum. Evol.*, 4, No. 4, 297–322 (1975).
7 Childers, W. Morlin, *Anthropological J. Canada*, 12, 2–9 (1974).
8 Bada, J. L., Schroeder, R. A., and Carter, G. F., *Science*, 184, 791–793 (1974).
9 Bender, M. L., *Nature*, 252, 378–379 (1974).
10 Bada, J. L., *Nature*, 252, 379–381 (1974).
11 Bada, J. L., *Earth planet. Sci. Lett.*, 15, 223–231 (1970).
12 Bada, J. L., Kvenvolden, K. A., and Peterson, E., *Nature*, 245, 309–310 (1973).
13 Bada, J. L., Protsch, R., and Schroeder, R. A., *Nature*, 241, 394–395 (1973).
14 Williams, G. E., and Polach, H. A., *Bull. geol. Soc. Am.*, 82, 3069–3085 (1971).
15 Hart, M. W., *Bull geol. Soc. Am.*, 85, 1329–1332 (1974).
16 Bowler, J. M., Thorne, A. G., and Polach, H. A., *Nature*, 240, 48–50 (1972).
17 Oakley, K. P., *Frameworks for Dating Fossil Man*, 7 (Weidenfeld and Nicolson. London, 1969).

Estimates of speeds of dinosaurs

THE faster an animal walks or runs the longer, in general, are its strides. Many dinosaur tracks have been found from which stride lengths can be measured[1]. I have now obtained a relationship between speed, stride length and body size from observations of living animals and applied this to dinosaurs to achieve estimates of their speeds. The estimated speeds are rather low—between 1.0 and 3.6 m s^{-1}.

Estimates of the speeds of large dinosaurs must depend on data from smaller animals. A means of allowing for differences in size is offered by the theory of physical similarity[2].

If meaningful comparisons are to be made between animals of different sizes, an appropriate non-dimensional parameter is needed to serve as a criterion for physical similarity. The most familiar parameter of this type is the Reynolds number which applies in situations where inertia and viscous forces interact and is very important in aerodynamics. Less familiar to biologists is the Froude number, which applies to any situation where inertia and gravity interact, and is important in nautical engineering. The Froude number is u^2/gl where u is the velocity, g the acceleration of free fall and l a characteristic length (in nautical engineering, the hull length) which, in this application to terrestrial locomotion, is the height h of the hip from the ground. The Froude number then becomes u^2/gh.

Considerations of physical similarity predict that the movements of animals of geometrically similar form but of different sizes will be geometrically similar only when they move with the same Froude number u^2/gh (that is, when the squares of their speeds are proportional to their linear dimensions). Geometrically similar movements require equal values of λ/h (that is, their stride lengths also must be proportional to their linear dimensions). The theory of physical similarity further predicts that, even when the Froude numbers are not the same, λ/h will be a function of the Froude number, although this function is not defined; we are obliged to obtain this relationship by empirical methods. It should be noted that stride length λ in this paper means the distance between corresponding

points on successive prints of the same foot[3]; the term is used to mean half this distance in some accounts of dinosaur tracks.

Animals of different sizes are not geometrically similar; there seems, however, to be a rather widespread relationship between λ/h and u^2/gh (ref. 4). Figure 1a shows that for mammals as diverse as jirds, men and horses

$$\lambda/h \simeq 2.3(u^2/gh)^{0.3} \qquad (1)$$

Figure 1b shows that for man, and presumably for other animals, the relationship between stride length and speed is not appreciably different for firm ground and soft mud. Equation (1) can be written

$$u \simeq 0.25g^{0.5}\lambda^{1.67}h^{-1.17} \qquad (2)$$

so that u can be estimated from known values of λ and h. λ can be measured accurately from tracks but h can only be estimated from the size of the footprints (see below). Equation 2 shows that if h is overestimated by 10%, u will be underestimated by 11%.

The tracks to be considered were made by unidentified bipedal dinosaurs and sauropods. It is assumed in each case that the metatarsophalangeal joint rested on the ground, but the tarsometatarsal joint did not. If this is correct, the length of the hind footprint is 0.23–$0.28h$ for many bipedal dinosaurs of a wide range of sizes, both Theropoda and Ornithopoda, and about $0.25h$ for *Apatosaurus* (Sauropoda) (see for instance the photographs of skeletons in refs 5 and 6). It will therefore be assumed that hind footprint length is $0.25h$ in all cases.

All the data in Table 1 refer to trails of fairly evenly spaced footprints, indicating progression at fairly constant speed. The plan in ref. 7 from which some of the data are taken has

Fig. 1 Graphs on logarithmic coordinates of relative stride length (λ/h) against Froude number (u^2/gh). *a*, Data from travelling on firm ground or treadmills for men[10,11] walking and running, horses[12], jirds (*Meriones unguiculatus*, unpublished observations of S. N. G. Frodsham and R. McN. A.), elephant[12] (*Elephas maximus*) (●) and ostrich[12] (*Struthio camelus*) (○). *b*, New data for man walking and running on hard ground (○), sandy mud (◉) and soft mud (●) at Snettisham beach, Norfolk. The subjects were an adult man and, two children (aged 11 and 13), each of whom made 4–8 walks or runs at various speeds (in random order) over a 25 m course on each substrate. They made moderate footprints in the sandy mud and very deep ones in the soft mud, on which it was very difficult to run. The broken line on each graph is
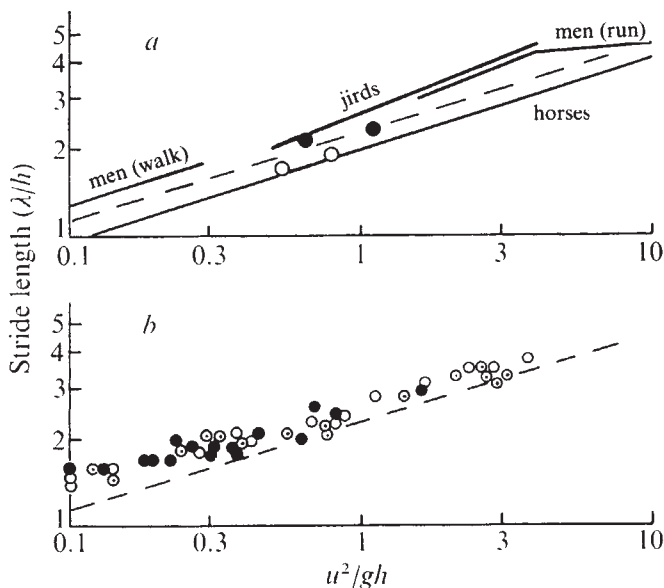
$$\lambda/h = 2.3(u^2/gh)^{0.3}.$$

Table 1 Dimensions of dinosaur tracks and data estimated from them

	Bipedal dinosaurs						Sauropods	
Reference	13	7	7	14	1	1	7	7
Stride length, λ (m)	3.0	3.0	2.4	1.3	1.8 –2.5	1.5 –1.8	2.5	1.6
Hind foot length (m)	0.53	0.50	0.24	0.27*	0.28–0.35	0.15–0.20	0.76	0.38
Hip height, h (m)	2.1	2.0	1.0	1.1	1.1 –1.4	0.6 –0.8	3.0	1.5
Relative stride length, λ/h	1.4	1.5	2.5	1.2	1.7	2.4	0.8	1.1
Speed, u (m s^{-1})	2.0	2.2	3.6	1.2	2.2	2.9	1.0	1.1

*Footprint length taken from measurements at the British Museum (Natural History). Other dimensions are taken from the published descriptions.

no scale but the paper includes a photograph of part of the same area marked out in yard squares, from which the scale has been determined. The speeds are rather low, especially those of the sauropods. Large and small sauropods seem to have been walking at the same speed, consistent with the suggestion that they were travelling as a herd[1,7].

Mammals generally change from a walk to a run or trot when the Froude number reaches about 0.6 and λ/h reaches 2.0 (ref. 4). Of the tracks recorded in Table 1, only the two fastest seem to show running, and both were made by fairly small dinosaurs. This does not necessarily mean that large dinosaurs never ran, but it seems to conform better with the traditional image of lumbering dinosaurs than with that of the lively runners shown in some recent restorations[8,9].

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1 Ostrom, J. H., *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 11, 287–301 (1972).
2 Duncan, W. J., *Physical Similarity and Dimensional Analysis* (Arnold, London, 1953).
3 Gray, J., *Animal Locomotion* (Weidenfeld & Nicolson, London, 1968).
4 Alexander, R. McN., in *Scale Effects in Animal Locomotion* (edit. by Pedley, T. J.) (Academic, London, in the press).
5 Kurtén, B., *The Age of Dinosaurs* (Weidenfeld & Nicolson, London, 1968).
6 Müller, A. H., *Lehrbuch der Paläozoologie*, 3(2) (Fischer, Jena, 1968).
7 Bird, R. T., *Nat. Hist., N.Y.*, 53, 60–67 (1944).
8 Bakker, R. T., *Discovery, Peabody Mus.*, 3, 11–22 (1968).
9 Galton, P. M., *J. Palaeont.*, 44, 464–473 (1970).
10 Cavagna, G. A., Margaria, R. and Arcelli, E., *Research Film*, 5, 309–319 (1965).
11 Zarrugh, M. Y., Todd, F. N. and Ralston, H. J., *Eur. J. appl. Physiol.*, 33, 293 306 (1974).
12 Muybridge, E., *Animals in Motion* (edit. by Brown, L. S.) (Dover Books, New York, 1957).
13 Albritton, C. C., *Fld Lab.*, 10, 161–181 (1942).
14 Charig, A. J. and Newman, B. H., *New Scientist*, 14, 234–235 (1962).

Stereoscopic vision within the schizochroal eye of trilobites

MOST trilobites had holochroal eyes which were probably analogous with the compound eyes of most living arthropods[1]. Trilobites of the suborder Phacopina had schizochroal eyes, in which comparatively few large separate lenses are distributed over the eye surface. Clarkson and Levi-Setti[2] showed that the schizochroal eye is unique in structure, in that each lens is biconvex and is made of two calcitic elements of different refractive indices, separated by an aspherical surface with a configuration such that the lens was corrected for spherical aberration. A modified interpretation by Campbell[3] suggests that the e and o rays were transmitted through the calcite lens to focus in the same plane. Since chromatic aberration is not important in seawater more than a few metres deep, either interpretation implies that each lens of the schizochroal eye was capable of forming an accurate image of its field of vision[2,3].

We suggest that the schizochroal eye was adapted to give

stereoscopic vision by the comparison and integration of optically accurate images from lenses within the same eye. Stereoscopic vision depends on the simultaneous perception of the same field of view through two lenses set at some distance apart. The images produced by the lenses should be of sufficient optical quality to define objects at useful resolution, the images should overlap considerably and there should be appropriate neural structures to interpret the information provided by the overlapping images. Towe[4], Clarkson and Levi-Setti[2] and Campbell[3] have already established the optical quality of the lenses. It remains to be shown that there would have been useful overlap between the images produced by adjacent lenses, and that it is reasonable to infer the existence of a suitable neural network behind the eye.

Clarkson[5,6] has measured the angular separation between the axes of the lens on many schizochroal eyes. The vertical spacing between lens axes is typically 2–10°, whereas the horizontal spacing is typically 7–20°. Since no part of the visual field is left unscanned, the cone of useful vision of a typical schizochroal lens would have been about 15–20° (for comparison, the ommatidia of *Limulus* have a useful range within 10–20° of their optic axes[7]).

The approximate hexagonal packing of lenses on the schizochroal eye usually included files of lenses arranged dorso-ventrally. Coupled with the astigmatism of the eye surface, this meant that the dorso–ventral files of lens axes formed "visual strips"[5]—files of lens axes with low angular separation, running nearly vertically across the visual field, each file of lenses separated by a significant angle from the next file. If each lens had an effective visual field of 15–20°, the visual fields of neighbouring lenses on each visual strip would have overlapped greatly, whereas the visual field of any given lens would only have overlapped marginally with its nearest neighbour on the next visual strip. Thus, given appropriate neural integration, the potential for stereoscopic vision was very great within each visual strip, but must have been marginal between strips.

We suggest that the large horizontal spacing between visual strips was such as to ensure that the whole visual field of the eye was scanned adequately, while the close vertical separation between lens axes along the visual strips allowed stereoscopic scrutiny over the whole visual field. Some phacopids had eyes in which the angular separation between lenses on visual strips approached the separation between strips. The arguments developed here would comfortably include these species, since the angles involved are never more than 6–7° (ref. 6), and would have permitted stereoscopic integration between lenses on the strips.

Rudwick and Clarkson[8] have shown how a trilobite might have detected an approaching object as it appeared successively on images produced by different lenses. In the ideal case, any array of closely spaced lens axes—as in a holochroal eye—would have been able to detect approaching objects with equal sensitivity. But in the real world of the trilobite, stereoscopic scrutiny by cooperating lenses arranged in files would more accurately have detected the